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CO_2-Enhanced Yield and Foliar Deformation among Tomato Genotypes in Elevated CO_2 Environments[1]

Kim E. Tripp, Mary M. Peet*, D. Mason Pharr, Daniel H. Willits, and Paul V. Nelson

Department of Horticultural Science (K.E.T., M.M.P., D.M.P., P.V.N.), Department of Biological and Agricultural Engineering (D.H.W.), North Carolina State University, Raleigh, North Carolina 27695-7609

ABSTRACT

Yield increases observed among eight genotypes of tomato (*Lycopersicon esculentum* Mill.) grown at ambient CO_2 (about 350) or 1000 microliters per liter CO_2 were not due to carbon exchange rate increases. Yield varied among genotypes while carbon exchange rate did not. Yield increases were due to a change in partitioning from root to fruit. Tomatoes grown with CO_2 enrichment exhibited nonepinastic foliar deformation similar to nutrient deficiency symptoms. Foliar deformation varied among genotypes, increased throughout the season, and became most severe at elevated CO_2. Foliar deformation was positively related to fruit yield. Foliage from the lower canopy was sampled throughout the growing season and analysed for starch, K, P, Ca, Mg, Fe, and Mn concentrations. Foliar K and Mn concentrations were the only elements correlated with deformation severity. Foliar K decreased while deformation increased. In another study, foliage of half the plants of one genotype received foliar applications of 7 millimolar KH_2PO_4. Untreated foliage showed significantly greater deformation than treated foliage. Reduced foliar K concentration may cause CO_2-enhanced foliar deformation. Reduced K may occur following decreased nutrient uptake resulting from reduced root mass due to the change in partitioning from root to fruit.

CO_2 enrichment of greenhouse crops has been used to increase productivity for over 100 years. Increased yield and increased CER[2] have been observed in most greenhouse crops grown at elevated CO_2, including tomato (*Lycopersicon esculentum*, Mill.) (26). Yield increases with CO_2 enrichment are generally attributed to increased CER. These increases in plant productivity can vary substantially with genotype (19, 21). The relationship between increased CER and increased yield among tomato genotypes with varying increases in yield at elevated CO_2 has not been specifically explored.

Some crops, including tomato, exhibit an additional response to long-term CO_2 enrichment, which is a deformation and discoloration of foliage (16). In tomato, this foliar deformation appears as a combination of discolorations reminiscent of K, Mg, and Mn deficiencies (22) accompanied by tight inrolling and malformation of the leaf lamina. The deformation appears first in the lower leaves and progresses to the upper leaves over the growing season until the entire plant appears stressed and dysfunctional. This apparent stress seems inconsistent with the increased yield found at elevated CO_2. Interactions of this apparently stressful response with other responses to CO_2 enrichment have not been studied. This report investigates the relationship between CER and plant productivity among eight genotypes of tomato exhibiting a range of yield responses to CO_2 enrichment. Potential relationships between CER, yield, degree of foliar deformation, and foliar nutrient status are explored in terms of the range and differences in response of the eight tomato genotypes.

MATERIALS AND METHODS

Genotype Response Differences, Foliar Deformation, and Foliar Nutrient Concentration

Plant Culture

Eight genotypes of greenhouse tomato, (*Lycopersicon esculentum*, Mill.), "B83.977," "Caruso," "Dombito," "Hotset," "Laura," "Michigan-Ohio," "Perfecto," and "TRVE13" were grown to transplant size in a glasshouse. Plants were watered two to three times daily, at need. Once a week, plants were watered with a liquid fertilizer (20–20–20) to saturation. At 7 weeks, seedlings were transplanted into 18.9 L black polyethylene grow-bags (Hydro-Gardens, Colorado Springs, CO) filled with 50% (v/v) Pro-Mix BX[3] (Premier Brands, New Rochelle, NY) and 50% aged, 95 mm mesh pine bark (v/v). Six plants of each genotype were transplanted to each of the four treatment greenhouses (48 plants per house). Experiments were conducted in four small, polyethylene-covered greenhouses in Raleigh, NC. Two houses were enriched to 1000 $\mu L \cdot L^{-1}$ CO_2. The remaining houses were at ambient CO_2 (about 350 $\mu L \cdot L^{-1}$). Rockbed storages (25) in the enriched houses allowed CO_2 enrichment to extend into the warm season. Average hours of CO_2 enrichment per day were 8.13. Details of greenhouse construction, CO_2 enrichment, rockbed storage systems, and environmental controls were reported by Willits and Peet (24). Day and night heating began at 21°C and 16°C, respectively. Cooling began at 25°C, 27°C, and 28°C for low and high vent and evaporative cooling pad, respectively.

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[2] Abbreviation: CER, carbon exchange rate.

[3] The use of trade names in this publication does not imply endorsement by the North Carolina Agricultural Research Service of products named nor criticism of similar ones not mentioned.

Plants were grown for 16 weeks in the treatments. The growing apex of all plants was removed after the sixth flower cluster had set at least one fruit. All axillary leaf growth was removed weekly. Fruit were harvested from all plants as they reached the pink stage (about three times a week). Fruit weights were recorded at each harvest on a plant-by-plant basis.

The experimental design was split-plot with whole plots of CO_2 concentration (greenhouses) and subplots of genotype. Whole plots were replicated twice (two houses at ambient and two houses at elevated CO_2).

Foliar Deformation Severity Rating

A visual rating of foliar deformation severity was developed to allow comparison of relative foliar deformation with other measured parameters (23). Weekly ratings of general foliar deformation were made on the lower canopies of all plants. Severity was rated on a scale of 0 to 3 where 0 = none, 1 = low, 2 = moderate, and 3 = severe. A rating of 1 was applied to plants in which approximately 1 to 33% of the canopy under evaluation was affected by deformation. A rating of 3 was applied to plants in which approximately 66 to 100% of the canopy was affected. Correlation analysis of mean deformation severity and mean total cumulative yield per plant of each genotype at ambient and elevated CO_2 was performed.

Net Photosynthesis (CER)

Foliar CER was measured using an LCA-2 portable leaf chamber analyzer system, A120 (Analytical Development Corporation, Andover, MA). All readings were taken between 0900 and 1500 h using natural light, during clear, full-sun conditions at 13 and 19 weeks plant age. Readings were taken on unshaded terminal leaflets of one leaf in the upper, middle, and lower third of the canopies of three plants of each of four genotypes in each house. Light levels were in the range of 650 to 1000 μmol m^{-2} s^{-1}. Readings were taken on only the cultivars "Michigan-Ohio," "Laura," "Hotset," and "TRVE13" in order to have adequate replication of a given genotype on a single sample date. These four genotypes were chosen because they exhibited the widest range of deformation response.

Fresh Weight Partitioning

Individual plant, leaf, stem, root, and fruit fresh weights were measured on four randomly chosen plants of each genotype in each house. Plant biomass was calculated as the sum of these four fresh weights. Leaves and stems were harvested and weighed at 23 weeks of plant age. Root balls from the same plants were removed from the grow bags, washed in water, squeezed to remove excess water, and weighed. Fruit fresh weights were calculated as cumulative total fruit weight harvested over the entire season on an individual plant basis.

Seed Number

When plants were 17 weeks old, two fruit were harvested from each of four genotypes in each house. Fruit were harvested at the mature green-pink stages. The genotypes used were the same four used for CER measurements as described above. Each of the four fruit per treatment were quartered and two opposite quarters were labeled and stored at −80°C. At a later date the fruit quarters were soaked in 10% (v/v) acetic acid for 30 min. Seeds were counted after separation from the remaining attached pulp by vigorously rinsing them in a sieve. Data are presented as mean seed number per fruit for each genotype at elevated and ambient CO_2.

Nutrition

Using drip irrigation, a modified Hoagland solution was injected into the watering lines 3 times daily for a total of 1.5 L, but waterings were increased or decreased depending on crop evapotranspiration. Fertilizer was delivered at each watering. Initial concentrations were 90 ppm N, 45 ppm P, 195 ppm K, 155 ppm Ca, and 44 ppm Mg. At apex removal, N and Ca were raised to 125 ppm N and 185 ppm Ca. Two weeks before crop removal, N and K were raised to 165 ppm N and 310 ppm K. Every 2 to 3 weeks fertilizer solutions were analyzed for nutrient content.

The terminal and one subtending leaflet of representative lower leaves were sampled for nutritional analysis at 1000 h when plants were 10, 11, 13, 14, 15, 17, 19, 21, and 23 weeks old. All leaflets for a given genotype in each house were pooled into one sample, dried at 70°C in a forced-air oven, and ground in a Wiley mill through a 20 mesh sieve. The air-dried tissue was analyzed for K, Ca, Mg, Mn, and Fe content by atomic absorption spectrophotometry (Perkin-Elmer Corp., Norwalk, CT) after dry ashing at 500°C. P content was analyzed using a spectrophotometric method (7).

The high foliar starch concentration of plants grown at elevated CO_2 has a dilution effect on foliar nutrient concentrations (8). Nutrient concentrations are artificially depressed when calculated on a dry weight basis because of the starch which makes it appear as though less nutrient was available to the tissue than actually was present (3, 12). Therefore, nutrient concentrations were corrected for starch by subtracting the milligrams of starch in a given leaf sample from the total milligrams of sample dry weight and then recalculating the nutrient concentration (12).

Foliar Starch Concentration

One leaf punch was taken from the same leaflets sampled for nutrient analysis before nutrient sampling and leaf starch concentrations were determined as described (23).

Foliar Nutrient Application Study

One genotype of greenhouse tomato, "Laura," was seeded and grown to transplant size in a glasshouse. Cultural practices were as described for the above study except that this study was conducted in one large polyethylene-covered greenhouse in Raleigh, NC, at ambient CO_2 (about 350 $\mu L \cdot L^{-1}$). Drip irrigation was used as described above. Foliar application of 7 mM KH_2PO_4 was made when plants were 13 to 20 weeks old. The solution was applied at 0900 h on one upper and

one lower leaf of 11 plants daily for 2 weeks and three times a week thereafter. Foliar deformation ratings were made weekly on the treated leaves of the 11 treated plants and on analogous leaves of 11 untreated plants. Mean foliar deformation of treated and untreated lower leaves is reported because little deformation developed on the upper leaves regardless of treatment.

RESULTS

Genotype Response Differences, Foliar Deformation, and Foliar Nutrient Concentration

Deformation and Yield

CO_2 enrichment increased both fruit yield and leaf deformation. Genotypes differed significantly in mean yield and deformation severity (Table I). Regression analysis showed a significant, positive relationship between mean foliar deformation severity and mean seasonal, total fruit yield such that the highest yielding genotypes showed the greatest foliar deformation severity (Fig. 1).

Net Photosynthesis (CER)

CERs were highest in the upper canopy, low in the middle canopy, and lowest in the lower canopy (Fig. 2). At 13 weeks plant age CERs were significantly greater in CO_2-enriched plants, but this was not the case at 19 weeks. CERs were negative in the middle and lower canopy region at 19 weeks and this was not improved by CO_2 enrichment (Fig. 2B). There were no significant differences between genotypes on either date and no apparent relationship with deformation.

Table I. *Mean Cumulative Fruit Yield per Plant and Mean Foliar Deformation Ratings for Eight Genotypes of Tomato Grown for 16 Weeks at Ambient (about 350 $\mu L \cdot L^{-1}$) or 1000 $\mu L \cdot L^{-1}$ CO_2*

Fruit yields and deformation ratings are the seasonal means for 12 plants.

CO_2	Genotype	Yield	Deformation[a]
$\mu L \cdot L^{-1}$		*g fresh wt·plant*$^{-1}$	
1000	TRVE13	7832	1.97
	Laura	7816	1.82
	B83.977	7838	1.68
	Michigan-Ohio	7750	1.55
	Perfecto	7480	1.59
	Dombito	7092	1.53
	Caruso	7373	1.47
	Hotset	7120	0.93
350	TRVE13	7110	1.61
	Laura	6743	0.96
	B83.977	7280	1.09
	Michigan-Ohio	5781	0.57
	Perfecto	5677	0.95
	Dombito	6432	0.82
	Caruso	6866	0.93
	Hotset	6258	0.47
LSD (P = 0.05):		521	0.05

[a] Deformation index: 0 = none, 3 = severe.

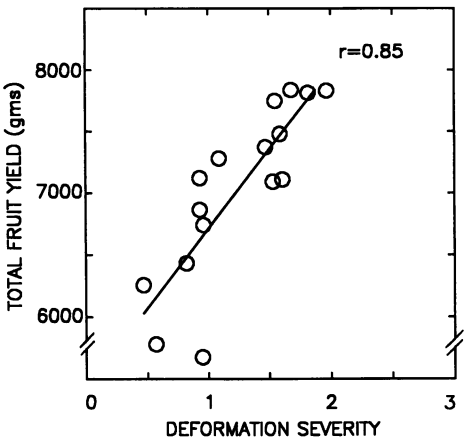

Figure 1. Linear regression relationship between mean foliar deformation severity (0 = none, 1 = low, 2 = moderate, 3 = severe) and mean seasonal total fruit yield (g per plant) of eight genotypes of tomato grown at ambient (about 350 $\mu L \cdot L^{-1}$) and 1000 $\mu L \cdot L^{-1}$ CO_2 for 16 weeks. Each point is the mean of 12 plants.

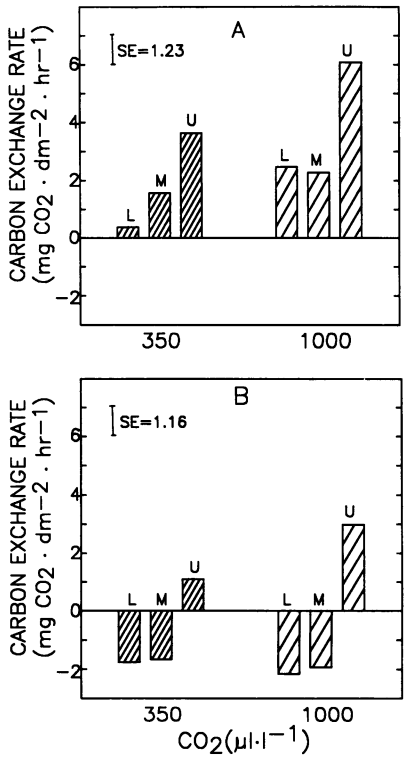

Figure 2. Mean foliar carbon exchange rates (mg $CO_2 \cdot d\ m^{-2} \cdot h^{-1}$) at 13(A) and 19(B) weeks plant age of the lower (L), middle (M), and upper (U) canopy regions of tomato plants grown at ambient (about 350 $\mu L \cdot L^{-1}$) and 1000 $\mu L \cdot L^{-1}$ CO_2. Each rate is the mean of readings on 24 leaves.

Fresh Weight Partitioning

Total plant biomass increased to only a small degree with CO_2 enrichment in all genotypes (Table II). CO_2 enrichment increased fruit fresh weight and decreased root fresh weight in all genotypes (Table III). Stem and leaf fresh weights both increased and decreased (depending on genotype) to small degrees with CO_2 enrichment. Linear regression analysis showed a significant negative relationship between fruit and root fresh weights but no relationship between fruit and leaf or stem fresh weights (Fig. 3).

Table II. *Mean Total Plant Biomass of Eight Genotypes of 23 Week Old Tomato Plants Grown at Ambient (about 350 $\mu L \cdot L^{-1}$) and 1000 $\mu L \cdot L^{-1}$ CO_2 for 16 Weeks*

Total plant biomass is calculated as the sum of a plant's leaf, stem, root, and cumulative fruit yield fresh weights. Each biomass is the mean fresh weight of eight plants.

Genotype	Biomass at 350 $\mu L \cdot L^{-1}$ CO_2	Biomass at 1000 $\mu L \cdot L^{-1}$ CO_2
	g fresh wt·plant^{-1}	
B83.977	9,426	9,928
Caruso	9,294	9,565
Dombito	8,556	9,427
Hotset	8,742	9,384
Laura	9,185	9,705
Mighican-Ohio	8,093	9,786
Perfecto	8,745	9,528
TRVE13	9,689	10,130

LSD (P = 0.05): 820.

Table III. *Mean Fruit, Root, Leaf, and Stem Fresh Weights of 23 Week Old Plants of Eight Genotypes of Tomato Grown for 16 Weeks at Ambient (about 350 $\mu L \cdot L^{-1}$) or 1000 $\mu L \cdot L^{-1}$ CO_2*

Each fresh weight is the mean of eight plants.

CO_2	Genotype	Fruit	Root	Leaf	Stem
$\mu L \cdot L^{-1}$			*g*		
350	B83.977	7335	743	919	427
	Caruso	6978	877	977	460
	Dombito	6283	801	1020	450
	Hotset	6143	861	1255	482
	Laura	6715	786	1196	482
	Michigan-Ohio	5624	996	1092	465
	Perfecto	6284	903	1092	465
	TRVE13	7123	745	1371	448
1000	B83.977	8023	537	918	449
	Caruso	7547	649	908	460
	Dombito	7317	533	111	464
	Hotset	7256	475	1180	471
	Laura	7579	411	1226	487
	Michigan-Ohio	7845	416	1099	455
	Perfecto	7482	420	1148	476
	TRVE13	7782	519	1369	459
LSD (P = 0.05):		568	209	93	31

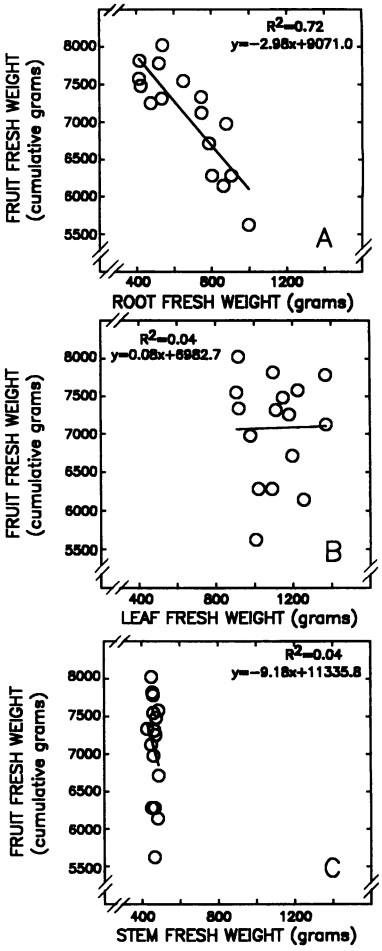

Figure 3. Linear regression relationship between fruit fresh weight (mean cumulative yield, g per plant) and root (A), leaf (B), and stem (C) fresh weights (g per plant) of eight genotypes of 23 week old tomato plants grown at ambient (about 350 μL) or 1000 $\mu L \cdot L^{-1}$ CO_2 for 16 weeks. Each point is the mean of eight plants.

Seed Number

CO_2 enrichment increased mean seed number per fruit in all genotypes (Fig. 4). All increases were statistically significant except for the genotype "Laura."

Nutrition

Over the season, K was the only element concentration reduced at elevated CO_2 after starch correction, but K, P, Ca, and Mg varied with genotype (Table IV). Mean K and Mn were significantly correlated with mean deformation (Table V) but only K was significantly correlated with deformation when correlation analysis was performed on the total data set (before averaging) (data not shown). Foliar deformation increased over the season and foliar K decreased in a parallel manner (Fig. 5).

Foliar Nutrient Application

Foliage treated with KH_2PO_4 showed less severe deformation than untreated foliage. Deformation increased over time

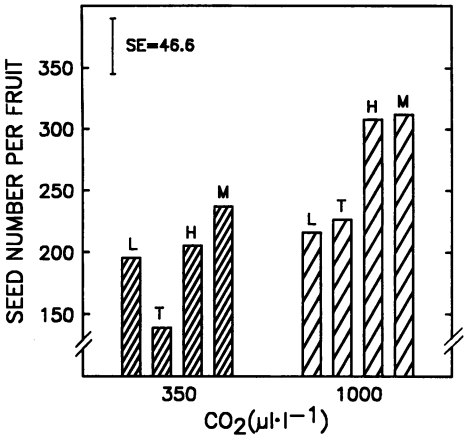

Figure 4. Mean seed number per fruit of four genotypes (L = "Laura," T = "TRVE13," H = "Hotset," M = "Michigan-Ohio") of 17 week old tomato plants grown for 10 weeks at ambient (about 350 $\mu L \cdot L^{-1}$) and 1000 $\mu L \cdot L^{-1}$ CO_2. Each count is the mean of four fruit.

in both treatments but remained less severe in treated foliage than in untreated foliage (Fig. 6).

DISCUSSION

These results show that in tomato, enhancement of yield with CO_2 enrichment was not due to increased CER. While the eight genotypes differed significantly in fruit yield, they did not differ in CER and there was no correlation between CER and yield. These results contrast with those of Nilwik *et al.* (18) who reported that maximum net photosynthesis varied with tomato genotype at elevated CO_2. The results are consistent with those of Lakso *et al.* (13), who also found no genotypic variation in CER. Nilwik *et al.* (18) measured photosynthesis only on plants much younger than those in this report. Therefore, their results may have been due to genotype differences which are only found early in the plants' development. An overall growth increase cannot be the primary cause of fruit yield increase with CO_2 enrichment. There was little increase in total plant biomass with CO_2 enrichment (about 8%) yet fruit yield increases were significantly greater (as much as 39%).

Instead, a change in partitioning from root to fruit was the primary mechanism for yield enhancement with CO_2 enrichment. CO_2 enrichment caused decreased root weight and increased fruit weight which varied with genotype. These results contrast with those of Knecht and O'Leary (11) who found no change in fresh weight of tomato root with CO_2 enrichment to 800 or 1200 $\mu L \cdot L^{-1}$. Knecht and O'Leary (11), however, sampled only after 4 and 7 weeks of treatment.

Table V. *Correlation Coefficients (r, n = 16)* and Probability Values (P) between Mean Foliar Nutrient Concentrations Corrected for Foliar Starch Concentration and Mean Foliar Deformation Severity for Plants of Eight Tomato Genotypes Grown at Ambient (about 350 $\mu L \cdot L^{-1}$) or 1000 $\mu L \cdot L^{-1}$ CO_2

Nutrient	r	P
K	−0.54	0.02
Ca	−0.30	0.25
Mg	−0.13	0.62
P	−0.10	0.68
Fe	−0.25	0.34
Mn	−0.74	0.01

Table IV. *Seasonal Mean Foliar Concentration of K, Ca, Mg, P, and Fe and Mn, Corrected for Foliar Starch Concentration, and Mean Foliar Deformation of Eight Tomato Genotypes Grown at Ambient (about 350 $\mu L \cdot L^{-1}$) or 1000 $\mu L \cdot L^{-1}$ CO_2*

Each concentration is the mean of 18 samples.

CO_2	Genotype	K	Ca	Mg	P	Fe	Mn	Deformation[a]
$\mu L \cdot L^{-1}$			% of dry weight			ppm		
350	B83.977	3.49	7.00	0.84	0.76	144	353	1.16
	Caruso	3.35	7.42	0.93	0.90	158	372	0.92
	Dombito	3.36	7.85	0.98	0.84	147	358	0.82
	Hotset	4.43	6.59	0.91	0.90	148	340	0.46
	Laura	4.04	6.98	0.87	0.89	148	324	0.96
	Michigan-Ohio	4.09	7.41	0.84	0.92	151	413	0.57
	Perfecto	3.83	6.63	0.77	0.78	144	326	0.95
	Trve13	3.85	6.43	0.91	0.88	141	331	1.53
1000	B83.977	3.30	6.64	0.80	0.83	132	279	1.71
	Caruso	3.31	7.48	0.91	0.96	142	336	1.53
	Dombito	3.16	7.39	0.91	0.86	139	334	1.46
	Hotset	4.52	6.73	0.90	1.01	145	359	0.93
	Laura	3.24	6.99	0.87	0.79	158	321	1.82
	Michigan-Ohio	3.55	7.09	0.87	0.79	146	322	1.54
	Perfecto	3.79	6.47	0.78	0.84	146	318	1.58
	Trve13	3.77	6.47	0.92	0.95	148	285	1.94
LSD (P = 0.05):		0.25	0.32	0.05	0.06	15	25	0.72

[a] Deformation index; 0 = none, 3 = severe.

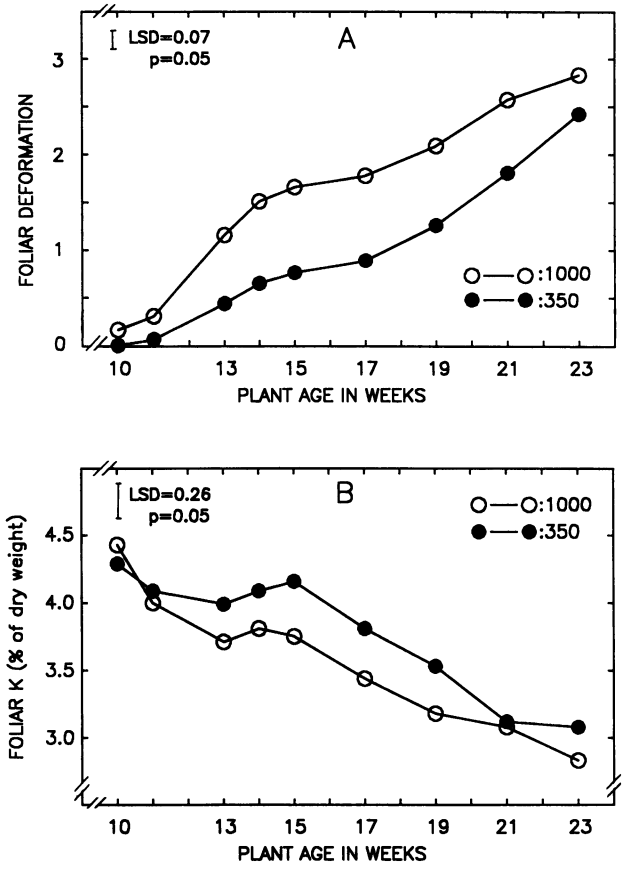

Figure 5. Mean foliar deformation severity (A: 0 = none, 1 = low, 2 = moderate, 3 = severe) and mean foliar K concentration (B: percentage of dry weight, corrected for foliar starch concentration) of lower canopy foliage of tomato grown at ambient (about 350 $\mu L \cdot L^{-1}$) or 1000 $\mu L \cdot L^{-1}$ CO_2. Each deformation point is the mean of ratings on 12 plants. Each K concentration point is the mean of 16 samples.

Therefore, they could not have reported any later effects on fresh weight partitioning as did our data after 16 weeks.

There was not a gram-for-gram correspondence between root fresh weight decrease and fruit fresh weight increase. This was probably because fruit fresh weights were cumulative over the season and therefore accounted for all fruits, but root fresh weights were measured once, destructively, at the end of the season. Therefore, root loss or regeneration during the season was not accounted for.

Altered partitioning of photoassimilates in CO_2-enriched environments has also been noted in *Cucumis* by Ito (6). He reported that cucumber plants with the longest exposure to elevated CO_2 had the least downward translocation of ^{14}C to the roots and the greatest translocation to the fruits. Ito suggested that improved early yields were due to the predominance of translocation to fruit over root in these plants.

In the present experiments with tomatoes there were strong genotypic differences in foliar deformation which showed a surprising, strong, positive relationship with yield. Genotypes appearing the most deformed and dysfunctional were the most productive in terms of fruit yield.

Foliar deformation with CO_2 enrichment has been attributed to high foliar starch concentration (1, 14). However, a seasonal comparison of foliar starch concentration and deformation severity in tomato showed no relationship between foliar starch and deformation (23). Instead, present results showed that the relationship between foliar deformation and foliar nutrient concentration was significant in terms of genotypic variation. Reduced K was associated with increased deformation.

The relationships between yield, partitioning, foliar deformation, and foliar nutrient concentration were observed through comparisons of genotypic differences. These genotypic differences may illustrate the mechanism for the observed change in partitioning and the relationships among all of these parameters.

Yield increases observed with CO_2 enrichment are consistent with many reports (9). The heavier fruit load observed in higher yielding genotypes may result in greater fruit sink strength than in lower yielding genotypes. Yelle *et al.* (28) reported interspecific differences in tomato fruit sink metabolism. In tomato, Ho (5) reported that assimilate translocation was regulated by sink demand. He observed that leaves with low carbon fixation rates maintained carbon export at the expense of existing carbon to keep up with sink demand. The increased sink strength may lead to the observed change in partitioning of nutrients and assimilates from root to fruit. Over an entire growing season, this change in partitioning could result in relatively reduced root mass in plants grown at elevated CO_2.

Reduced root mass under elevated CO_2 conditions could lead to decreased uptake of nutrients. Tomato fruit nutrient uptake may not be reduced in response to such a reduced nutrient supply. Halbrooks and Wilcox (4) found that K uptake into tomato leaves increased until 70 d after anthesis and then decreased, but K uptake into fruit increased continuously over the entire period to 105 d after anthesis. Kirkby *et al.* (10) reported no difference in xylem sap K concentration of tomato plants grown at low (0.4 $meq \cdot L^{-1}$) or high (4 $meq \cdot L^{-1}$) K nutrient solution. They concluded that the highly mobile K ion was remobilized and translocated to sink areas which had constant K demand.

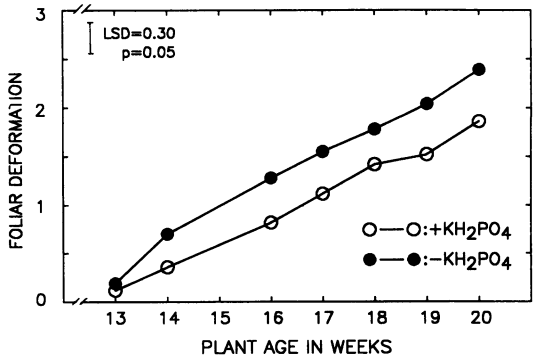

Figure 6. Mean foliar deformation severity (0 = none, 1 = low, 2 = moderate, 3 = severe) of tomato foliage grown at ambient (about 350 $\mu L \cdot L^{-1}$) CO_2 either treated or untreated with 7 mM KH_2PO_4 foliar spray. Each point is the mean of ratings on 11 leaves in the lower third of the canopy.

As a result, depletion of mobile elements, like K or possibly N, in older tomato leaves may result in the observed nutrient-deficiency-like symptoms of foliar deformation. McAvoy and Janes (15) observed foliar nutrient deficiency-like symptoms with high pressure sodium lighting. These symptoms were alleviated with increased nutrient supply. When nutrient supply is inadequate fruit nutrient demand would then be met by mobile element remobilization from other plant tissues. Wolterbeek and De Bruin (27) compared import of radiolabeled ions into tomato fruit from stem or leaf tissue and concluded that leaves were a primary source of element redistribution in tomato. Foliar application of K alleviated deformation symptoms. Therefore, remobilization of foliar K from older leaves of CO_2-enriched tomato plants in response to decreased K supply and unchanged or increased K demand by increased fruit load probably causes K deficiency-like symptoms in these older leaves. Fertilization with increased nutrient solution concentrations might not alleviate symptoms because the decreased supply is probably due to decreased root mass.

Some genotypes may respond to CO_2 enrichment with greater increase in sink strength than others and would therefore have greater yield and foliar deformation, accompanied by more reduced root mass and foliar nutrient concentration. A hypothetical mechanism to explain genotypic differences in CO_2 enhancement of sink strength could involve increased fertilization and seed set that varied with genotype. Dempsey and Boynton (2) have shown that increased seed number caused increased fruit size and, therefore, probably increased sink activity.

Our preliminary results showed increased mean seed number per fruit with CO_2 enrichment. CO_2 enrichment may increase fruit sink strength through increased fertilization and seed set. Sfakiotakis *et al.* (20) reported that the percentage of germination of lily pollen increased rapidly when CO_2 concentration was increased from ambient to 1.3%. There were increases at all CO_2 concentrations. Nakanishi *et al.* (17) observed increased pollen tube penetration of stigma papilla cells from self-pollinated, self-incompatible Brassica flowers following CO_2 treatment.

CO_2 enrichment resulted in a series of genotypically variable responses. These responses may be explained by a differential increase in seed set and, therefore, sink strength among the genotypes leading to mobilization of nutrient and assimilates to the fruit. Such a change in fruit sink strength could have caused the observed reductions in root mass and foliar nutrients. This intraplant competition could vary with genotype and may explain the observed genotypic differences in yield and foliar deformation observed with CO_2 enrichment.

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